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Pollination biology of the columnar cactus *Pachycereus pecten-aboriginum* in north-western México

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Abstract

Columnar cacti in tropical deserts depend on nectar-feeding bats for their reproduction while species from extra-tropical deserts show a relatively generalized pollination system with both nocturnal and diurnal pollinators. *Pachycereus pecten-aboriginum* is a columnar cactus with a broad distribution along the Pacific coast of México, from Oaxaca to Sonora. Along its distribution, the nectar-feeding bat, *Leptonycteris curasoae*, changes from resident within the tropics to migratory in the Sonoran desert. If bat unpredictability has been an important force in the evolution of pollination systems in columnar cacti, *P. pecten-aboriginum* is expected to show a relatively generalized system in northern populations. We studied the pollination biology of *P. pecten-aboriginum* in two northern populations in the state of Sonora. Hand pollination experiments showed that this species has a self-incompatible, hermaphroditic breeding system. Although flowers open at night, they remain open and continue secreting nectar during the morning, allowing visitation by both nocturnal and diurnal pollinators. One population showed evidence of strong pollinator limitation while the results from both populations indicated that diurnal pollinators are more important than nocturnal pollinators. These results are discussed in terms of specialization vs. generalization in the pollination biology of columnar cacti in tropical and extra-tropical deserts.

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1. Introduction

Plant pollination systems are thought to form a continuum from highly specialized systems with a single pollinator to generalized systems with hundreds of pollinator species (Johnson and Steiner, 2000). As angiosperms are thought to occupy virtually every point on the continuum, it is important to understand the ecological forces that have favored generalization or specialization in particular lineages and regions (Johnson and Steiner, 2000). Columnar cacti represent a lineage where clear trends toward generalization have been identified. Pollination experiments conducted within and outside the tropics have revealed a clear geographical pattern. Pollination experiments conducted in the Tehuacán Valley in México showed that bats are the major pollinators of columnar cacti (Valiente-Banuet et al., 1996, 1997a, b). In contrast, pollination experiments with columnar cacti in the Sonoran desert have shown that both bats and diurnal visitors (several species of birds and bees) are effective pollinators (Fleming et al., 1996, 2001). These studies reveal that columnar cacti show specialized pollination within the tropics (Valiente-Banuet et al., 1996, 1997a, b), and moderate generalization outside the tropics where they are pollinated by a variety of animals, including birds, bats, and insects (Fleming et al., 1996, 2001).

Valiente-Banuet et al. (1996) suggested that the geographical pattern in México reflect year-to-year variation in the abundance and reliability of the nectar-feeding bat, *Leptonycteris curasoae* (Phyllostomidae, Glossophaginae), at the northern limits of the distribution of columnar cacti. Capture records indicate that this nectar-feeding bat may be resident year-round in the tropics where resources are available throughout the year and migratory in extratropical deserts where resources are seasonally available (Rojas-Martínez et al., 1999). Furthermore, the abundance of *L. curasoae* in the Sonoran desert varies significantly within and among years (Fleming et al., 2001). Assuming asymmetric fitness trade-offs (Aigner, 2001), models of the evolution of pollination systems predict specialization whenever effective pollinators are predictably available in space and time and generalization when pollinators are temporally and spatially variable (Waser et al., 1996). Thus, if the abundance of *L. curasoae* varies annually and geographically, simple models would predict the evolution of a relatively generalized pollination system (a system involving both nocturnal and diurnal pollinators) at the northern edge of the distribution of columnar cacti.

Pachycereus pecten-aboriginum has probably the widest distribution in México among columnar cacti. It is distributed from the Isthmus of Tehuantepec (ca. 16°N) in the state of Oaxaca (Bravo-Hollis, 1978; Gama, 1994) to east central Sonora (ca. 29°N) and southern Baja California (Turner et al., 1995; see Fig. 1). Most of its current range of distribution is within the range where *L. curasoae* is thought to be resident (Rojas-Martínez et al., 1999). Its northern range, however, is where *L. curasoae* is migratory or transitional. Thus, if the abundance and predictability of *L. curasoae* has been an important force in the evolution of its pollination system (Valiente-Banuet et al., 1996), we would expect a relatively generalized system in the northern range. In this paper, we describe basic aspects of the pollination biology of

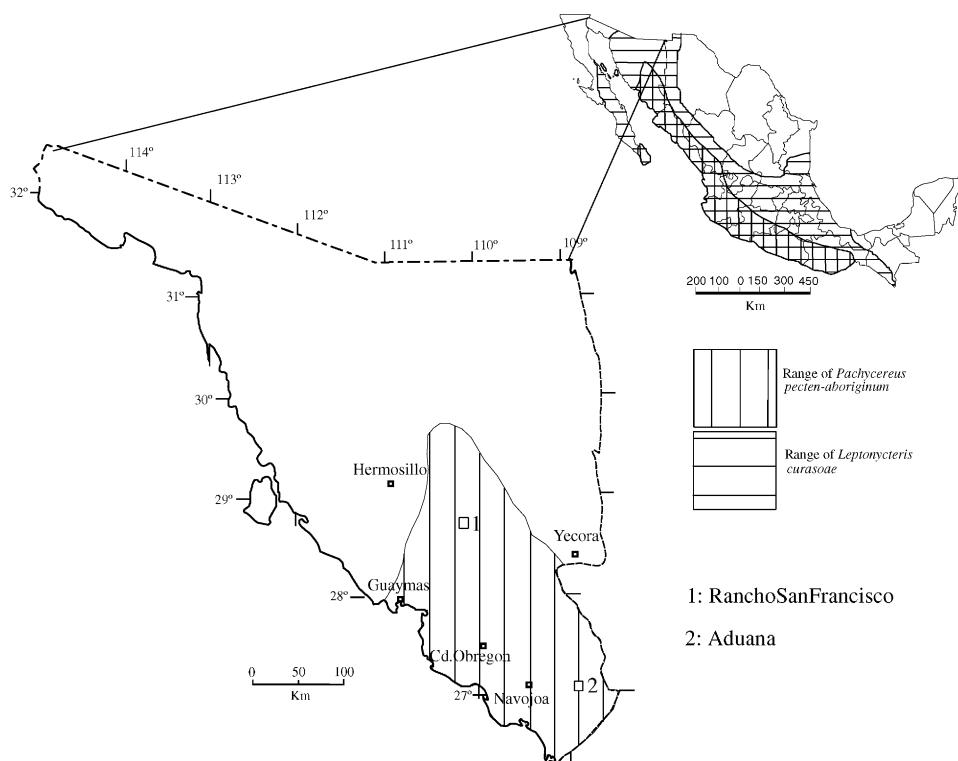


Fig. 1. Map showing the location of the study populations of *P. pecten-aboriginum* in the state of Sonora, México. Map on upper right corner shows the distribution of *P. pecten-aboriginum* (after Bravo-Hollis, 1978; Gama, 1994; Turner et al., 1995) and *L. curasoae* (after Medellín et al., 1997; Rojas-Martínez et al., 1999) in México.

two populations of *P. pecten-aboriginum* at the northern limits of its distribution in México.

2. Materials and methods

2.1. Study sites

We studied two populations of *P. pecten-aboriginum* in the state of Sonora at two different times: Aduana from February 8 to 17 in 1993 and Rancho San Francisco from January 24 to February 7 in 1998 (Fig. 1). Rancho San Francisco (28°41'N; 110°16'W) is located on km 84 along highway 16 (Hermosillo-Yécora), close to the town of San José de Pimas, Sonora. Aduana (27°03'N; 109°00'W) is a small village, 8 km SW of Alamos, Sonora. Vegetation in the Alamos region is classified as tropical deciduous forest (Martin et al., 1998). Annual precipitation in Alamos averages

about 640 mm, 75% or more falls during the June through October growing season (Gentry, 1982). Temperatures range from an average low of 17.8°C in the winter to an average high of 33.8°C just before the rains begin in the summer. At Rancho San Francisco, vegetation is classified as thornscrub. Annual precipitation in San José de Pimas averages 431 mm (1982–1997); 80% falls between June and September (Comisión Nacional del Agua, Delegación Hermosillo, Sonora). Temperatures range from 15°C in January to 31°C in July (Comisión Nacional del Agua).

2.2. Plant abundance, flowering intensity and flower availability

At Rancho San Francisco, we estimated the density of *P. pecten-aboriginum* by counting the number of juvenile and adult plants in 6 randomly located 50 × 50 m plots. We measured basal diameter, height of the major axis and number of branches on each plant. We defined flowering intensity as the frequency of flowering individuals in a sample of 25 multi-branched plants on 22 March 1996, 7 February 1998, 19 March 1998 and 11 February 1999. The number of open flowers per adult for a sample of 20 multi-branched plants was counted during three consecutive nights when pollination treatments were applied (see below) in order to estimate resource availability for pollinators.

At Aduana, we marked 37 adult plants growing on a hillside and recorded the number of branches (> 1 m). In mid-February and mid-March 1993, we recorded the number of open and recently closed flowers and the number of developing fruits on each plant.

2.3. Floral biology

At Rancho San Francisco, one flower from each of 28 plants was used for measuring flower dimensions. Measurements included flower length (i.e. from petal tip to flower base), external diameter at the corolla apex and internal diameter of floral tube at the point of anther dehiscence. We used this sample of 28 flowers to verify if they were hermaphrodite (i.e. we checked ovaries for ovules and anthers for pollen). In order to describe flower opening and closure, we measured the distance between opposite tepal tips in a sample of 12 flowers from 12 plants every 2 h beginning at bud opening. Flower receptivity was also recorded by monitoring anther dehiscence and stigma turgidity in 10 flowers from 10 plants every 2 h. Nectar volume secreted by flowers was measured from 2100 to 1400 h in a sample of 11 bagged flowers from nine plants. Nectar was extracted every 2 h using a graduated 1 ml syringe. Flowers were bagged before anthesis with bridal veil netting and were kept bagged after each measurement. Sugar concentration was also measured every 2 h with a hand-held refractometer (ERMA model 10040).

At Aduana, one about-to-open flower was collected from 25 plants and its ovules were removed and preserved in 70% ethanol for counting in the laboratory. Nectar production from flower opening until 1100 h the following morning was determined by removing nectar with a 1 ml syringe from 19 bagged flowers (see below). Sugar concentration of this nectar was determined using a field refractometer (Atago model

ATC-1E). On 30 April 1993, we counted the number of fruits on 25 plants and collected one large, nearly mature fruit from 10 plants and counted their mature (filled) seeds in the laboratory. To determine seed mass, we weighed groups of 10 mature seeds (to the nearest 0.1 mg) from eight fruits collected at San Carlos, Sonora, on 23 April 1992.

2.4. *Breeding system*

To determine whether flowers are self-compatible and the importance of nocturnal and diurnal pollinators, we conducted a pollination experiment in each population. Due to low flower production in Alamos, only three pollination treatments were employed at Aduana while six treatments were used at Rancho San Francisco. At Rancho San Francisco, the pollination experiment used a total of 326 tagged flowers in 6 pollination treatments distributed across 31 plants. Different numbers of flowers were assigned to each of the following treatments: (1) autonomous self-pollination ($n = 40$ flowers on 12 plants); buds were bagged with bridal veil netting (Wyatt et al., 1992) and left without manipulation until flowers closed. (2) Self-pollination ($n = 29$ on nine plants); flower buds were bagged; soon after the flowers opened they were hand-pollinated using pollen obtained from the same flower. (3) Diurnal pollinator exclusion ($n = 48$ on 22 plants); flower buds were tagged before opening and were exposed to nocturnal visitors at night and excluded from diurnal visitors by bagging flowers at sunrise. (4) Nocturnal pollinator exclusion ($n = 44$ on 19 plants); flower buds were bagged and remained unavailable to nocturnal visitors; flowers were exposed to diurnal visitors by removing the bag at sunrise until the flowers closed. (5) Cross-pollination treatment ($n = 33$ on 14 plants); flower buds were bagged; when flowers opened they were hand-pollinated by saturating the stigma with fresh pollen obtained from another plant. (6) Open-pollinated control ($n = 132$ on 31 plants); flowers that opened during 3 consecutive days were tagged; these flowers were available to nocturnal and diurnal visitors. The fate (aborted or developing fruit) of the tagged flowers from pollination treatments was scored on 19 March 1998. Fruits were monitored every 15 days until they matured. Mature fruits were collected in mid-June (11–15). In the lab, fruits were opened, and the air-dried pulp and seeds were separated. The mass of the entire lot of seeds from each fruit was determined to the nearest mg, and one group of 50 seeds per fruit was weighed to determine average seed mass. Total seed mass divided by average mass per seed provided an estimate of the number of seeds per fruit. At Aduana, pollination treatments were applied to 87 flowers distributed on 17 plants. Treatments were applied as before and included: (1) open-pollinated controls ($n = 36$ flowers on 16 plants); (2) self-pollinated flowers ($n = 28$ on 17 plants) and (3) nocturnal pollinator exclusion ($n = 23$ on 13 plants). The fate of the tagged flowers (aborted or developing fruit) was scored on 15 March 1993.

Fruit set among pollination treatments were analysed by means of a logistic model. The number of seeds per fruit and seed mass among treatments were analysed by means of a one-way ANOVA. All statistical analyses used JMP 3.1 software.

2.5. Flower visitors

At Aduana, flower visitors were identified during diurnal and nocturnal fieldwork. No animals were captured for pollen analysis.

At Rancho San Francisco, nocturnal and diurnal visitors were captured by placing ten mist nets (10 m long $\times$ 2 m tall; separated by $\approx$ 100 m) during 3 days across an area with a high density of *P. pecten-aboriginum*. For each animal caught, pollen preparations were made by rubbing a cube of fuchsin-stained jelly (Beattie, 1971) over the animal's body. The cube was placed on a microslide, melted, and covered with a coverslip for later examination under the microscope. Pollen presence was regarded as proof of flower visitation. Pollen grains from animal samples were later compared with those obtained from flowers of *P. pecten-aboriginum*.

3. Results

3.1. Plant abundance, flowering intensity and flower availability

At Rancho San Francisco, *P. pecten-aboriginum* had a mean density of 57.3 ± 10.9 (mean $\pm$ 1 S.D.) plants/ha. If only reproductive individuals (> 2 m tall) are considered, mean density was 36.0 ± 10.1 adults/ha. In this area, adult plants reach heights of 7–8 m, basal diameters of 0.5–0.6 m and number of fertile branches (> 1 m) of 40–45. Flowering intensity was high (0.92) during the period where pollination treatments were applied (5–7 February); by 19 March it had declined to 0.56. In contrast, flowering intensity was low on 22 March 1996 (< 0.10) and on 11 February 1999 (0.28). During three consecutive nights when pollination treatments were applied, adult (multi-branched) individuals produced from 9.6 ± 7.7 to 11.5 ± 9.1 (range: 1–35) flowers/plant.

At Aduana, adult plants of *P. pecten-aboriginum* attained heights of 10–12 m and bore on average 7.0 ± 6.1 ($n = 37$; range: 1–25) fertile branches. In mid-February 1993, flowering intensity was 0.89 and plants bore 3.4 ± 3.9 (range: 0–18) open flowers/plant. In mid-March, flowering intensity was 0.76 and plants bore 3.8 ± 4.5 (range: 0–22) flowers/plant.

3.2. Floral biology

At Rancho San Francisco, dimensions of flowers of *P. pecten-aboriginum* were: length = 7.7 ± 0.8 cm ($n = 28$); internal diameter 2.6 ± 0.3 cm; external diameter = 6.2 ± 0.6 cm. All dissected flowers were hermaphrodite. Flowers started to open at dusk (ca. 1900 h) and remained open to 0900 h when they gradually began to close (Fig. 2A). Anthers and stigmas were turgid throughout the night, maintaining an apparent turgidity up to 1400 h when pollen disappeared from anthers. Nectar production was continuous during flower anthesis until 1300 h (Fig. 2B) and no evidence was found that nectar was reabsorbed if not consumed by visitors. Sugar concentration ranged from 16.6% to 22.3% (Fig. 2C).

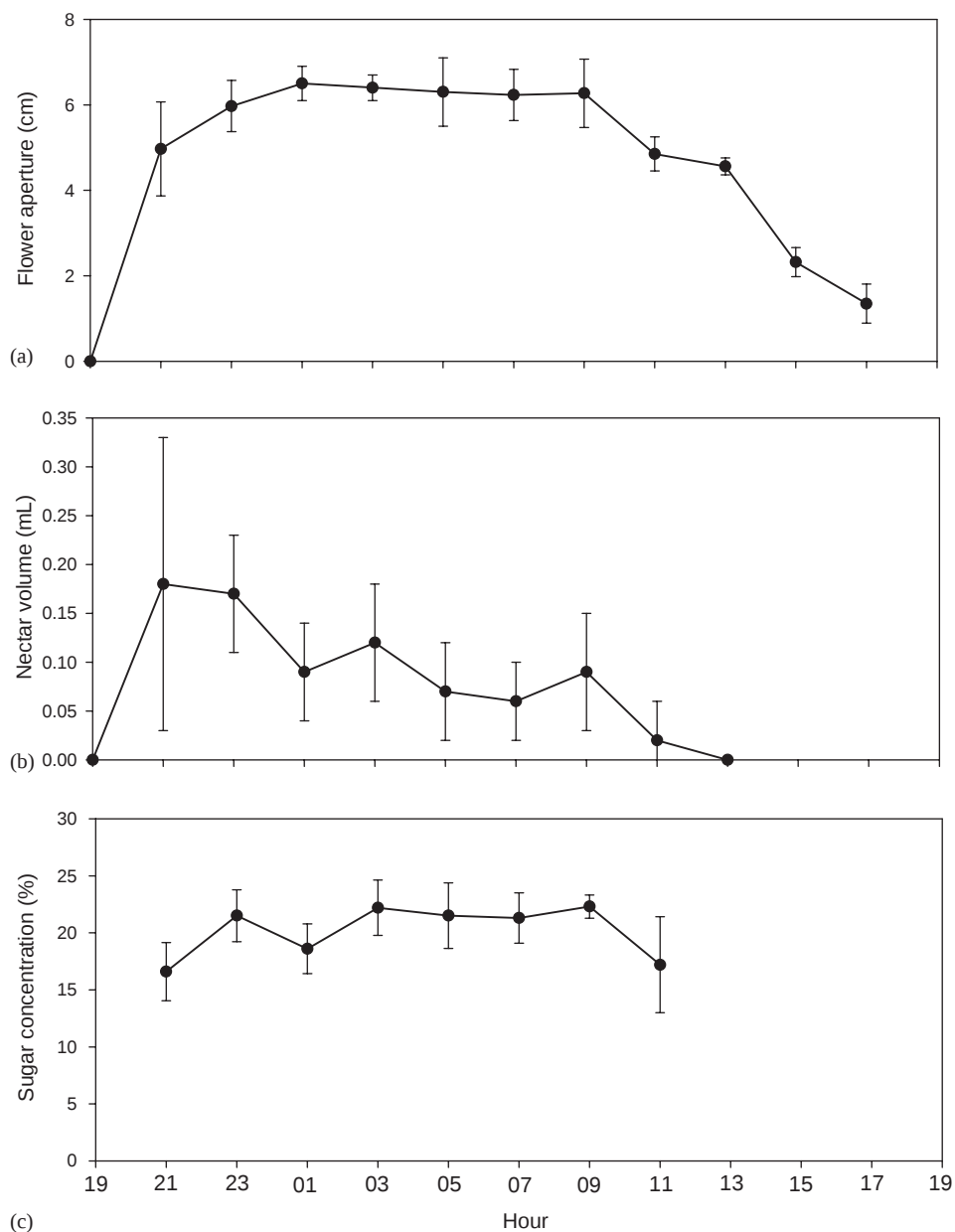


Fig. 2. Temporal pattern of opening, closing, nectar production and sugar concentration in flowers of *P. pecten-aboriginum* at Rancho San Francisco, Sonora. (A) Flower opening and closing in a sample of 12 flowers on 6–7 February 1998. (B) Nectar production in a sample of 11 flowers. (C) Sugar concentration in nectar extracted from a sample of 11 flowers. Bars indicate one standard deviation.

At Aduana, nectar volume averaged 0.74 ± 0.26 ml ($n = 19$; range: 0.31–1.36 ml) and sugar concentration in nectar averaged $20.6 \pm 1.73\%$ ($n = 19$; range: 16.0–23.5%). Flowers contained an average of 704.9 ± 228.3 ovules ($n = 25$; range: 438–1183), and open-pollinated fruits contained an average of 539.1 ± 106.9 seeds ($n = 10$; range: 367–665). Mature seeds weighed 16.0 ± 0.05 mg ($n = 8$ seed lots). In mid-February, 41% of our marked plants bore well-developed fruit, and 78% bore either immature or well-developed fruit. In mid-March, 97% bore well-developed fruit, and on 30 April, all plants bore at least one developing fruit. Total number of mature fruits per plant on 30 April was 54.1 ± 62.6 ($n = 37$; range: 1–293).

3.3. Breeding system

At Rancho San Francisco, none of the hand self-pollinated flowers of *P. pecten-aboriginum* set fruit (Table 1). Similarly, unmanipulated and visitor-excluded flowers did not set fruit. In the other pollination treatments fruit set was 5% in the diurnal-exclusion treatment, 18% in nocturnal-exclusion treatment, 26% in open-pollinated flowers and 77% in hand-cross pollination (Table 1). Highly significant differences were detected among pollination treatments ($\chi^2 = 29.6$; df. = 5; $p < 0.0001$). Differences between open-pollinated and cross-pollination treatments were significant ($\chi^2 = 13.2$; df. = 1; $p = 0.0003$). The number of seeds per fruit ranged from 100 for the diurnal-exclusion treatment to 409 for the hand cross-pollination treatment (Table 1). Differences between open-pollinated and cross-pollination treatments were also significant for the number of seeds per fruit ($F = 7.50$; $p = 0.01$). For seed mass, no significant differences were detected among treatments ($F = 0.0001$; $p = 0.99$).

At Aduana, none of the self-pollinated flowers ($n = 28$) set fruit. Fruit set in flowers from which bats were excluded was 55% ($n = 22$ flowers). Fruit set in open-pollinated flowers was 58% ($n = 36$).

Table 1

Fruit set, number of seeds per fruit and seed mass in different pollination treatments in a population of *P. pecten-aboriginum* at Rancho San Francisco

Pollination treatment	Fruit set	<i>N</i>	<i>n</i>	Number of seeds/fruit	Nfr	Mass of 50 seeds (g)
Autonomous self-pollination	0.00 (0.00)	12	40	0.0 (0.0)	—	
Manual self-pollination	0.00 (0.00)	9	29	0.0 (0.0)	—	
Nocturnal-exclusion	0.18 (0.08)	19	44	120.1 (85.9)	6	0.76 (0.30)
Diurnal-exclusion	0.04 (0.03)	22	48	100.0 (0.0 ^a)	1	—
Open-pollinated control	0.26 (0.35)	31	132	235.9 (167.3)	25	0.76 (0.15)
Manual cross-pollination	0.77 (0.10)	14	33	427.3 (197.8)	14	0.80 (0.15)

Values are means and numbers in parentheses indicate 1 S.D.; *N*: number of plants; *n*: number of flowers; Nfr: number of fruits.

^a Just one fruit was recovered.

3.4. Flower visitors

At Rancho San Francisco, only 1 individual of the nectar-feeding bat *L. curasoae yerbabuena* Martínez & Villa was caught; it bore pollen of *P. pecten-aboriginum*. Diurnal visitors caught bearing pollen of *P. pecten-aboriginum* included hummingbirds (2 *Hylocharis leucotis*; 1 *Calypte costae*; 1 *Cynanthus latirostris*), woodpeckers (6 *Melanerpes uropygialis*; 1 *Colaptes auratus*), finches (2 *Carpodacus mexicanus*), sparrows (7 *Zonotrichia atricapilla*), gnatcatchers (1 *Polioptila caerulea*), towhee (1 *Pipilo fuscus*), vireos (1 *Vireo solitarius*), verdins (4 *Auriparus flaviceps*), wrens (2 *Campylorhynchus brunneicapillus*), and bees (*Apis mellifera*). All hummingbirds, woodpeckers and the finch were observed consuming nectar directly from open flowers during the morning. In the case of woodpeckers and *C. mexicanus*, birds placed their heads in flowers and touched stigmas, whereas hummingbirds approached the flowers from the base robbing the nectar.

At Aduana, diurnal visitors included hummingbirds (*Amazilia violiceps* and *Cynanthus latirostris*), a woodpecker (*Melanerpes uropygiales*) and honeybees (*Apis mellifera*). Flowers were most likely visited at night by *L. curasoae*, but we collected no specimen to confirm this.

4. Discussion

Our results indicate that *P. pecten-aboriginum* has a self-incompatible, hermaphroditic breeding system. Pollination experiments in one population showed evidence of strong pollinator limitation and diurnal pollinators were more important than nocturnal pollinators in both populations. Thus, the pollination biology of northern populations of *P. pecten-aboriginum* resembles the relatively generalized pollination system of columnar cacti in the Sonoran desert.

In Tehuacán, columnar cacti depend on nectar-feeding bats for their reproduction. Anthesis is nocturnal and nocturnal-exclusion experiments indicate that diurnal visitors are not effective. Bats are reliable pollinators and as a consequence, no evidence of pollinator limitation has been detected (Valiente-Banuet et al., 1996, 1997a, b). In contrast, columnar cacti from the Sonoran desert have nocturnal flowers that remain open, secrete nectar, and are receptive during the day, allowing pollination by both nocturnal and diurnal visitors. The relative importance of nocturnal and diurnal pollinators thus varies in space and time, and when pollen limitation has been detected, the “missing” pollinator has been *L. curasoae* (Fleming et al., 1996, 2001). Our results at Rancho San Francisco indicate that *L. curasoae* was rare and likely to be the missing pollinator responsible for the low fruit set and lower number of seeds per fruit observed in open-pollinated flowers of *P. pecten-aboriginum*. Flowers were open and receptive during the day and several bird species were observed visiting them at both sites. Our pollination-exclusion experiments in both populations indicated that the contribution of nocturnal pollinators was low and that diurnal pollinators were responsible for a significant proportion of fruit set in both populations. This result is particularly revealing at Aduana, as this

population is within 1 km of a known roost site of *L. curasoeae*, where 20,000 adult bats were observed on 13 February 1993 (Wilkinson and Fleming, 1996).

Our results also provide evidence for an association between ploidy level and incompatibility systems in the genus *Pachycereus*. Available evidence indicates that gametophytic self-incompatibility is widespread within the subfamily Cactoideae (Boyle, 1997). Our results with *P. pecten-aboriginum* showed that this species has a self-incompatible, hermaphroditic breeding system. Evidence from chromosome counts (Pinkava et al., 1977) indicate that northern populations of this species are diploid. Similarly, studies on the pollination biology and chromosome numbers in *P. weberi* have shown that this species is diploid and has a self-incompatible, hermaphroditic mating system (Gama, 1994; Valiente-Banuet et al., 1997b). These studies reveal that diploid members of the genus *Pachycereus* are self-incompatible hermaphrodites. In contrast, chromosome counts (Pinkava et al., 1973) and isozyme segregation (Murawski et al., 1994) has shown that *P. pringlei* is autotetraploid. In this case, populations are gynodioecious or trioecious and hermaphrodites are self-compatible (Fleming et al., 1994, 1998). Thus, polyploidy seems to be associated with the breakdown of the incompatibility system in *Pachycereus*, as observed in other plant taxa (Levin, 1983). Studies of the breeding systems and chromosome numbers of other columnar cacti could provide evidence on whether this association is widespread in other lineages of the tribe Pachycereeae.

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